A Field Study of the Effects of Incline on the Escape Locomotion of a Bipedal Lizard, *Callisaurus draconoides*

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ABSTRACT

We analyzed footprints on the surface of a sand dune to estimate maximal running speeds and the incidence of bipedality in nature, as well as to investigate the effects of incline on the escape locomotion of the lizard *Callisaurus draconoides*. Previous laboratory tests predicted that inclines would negatively affect sprinting performance in *C. draconoides*. Although physiologists commonly assume that escape locomotion will be near maximal capacity, we found that only 11% of all strides were greater than 90% of maximal speed of *C. draconoides*. Escape paths averaged 10 m in length and were generally straight. Approximately 30% of the strides taken by *C. draconoides* were bipedal, and this value was three times greater than previously found for the closely related species *Uma scoparia*. The modal value of bipedal stride lengths was greater than that for quadrupedal strides. Inclines negatively affected velocity of only the first meter of *C. draconoides* escape paths. The location of nearest cover had better predictive value for the initial orientation of *C. draconoides* escapes than incline. On steep slopes (>15°), *C. draconoides* avoided running directly downhill and uphill and primarily ran horizontally, whereas on shallow slopes, lizards exhibited approximately equal amounts of horizontal, direct uphill, and direct downhill running.

Introduction

Rapid speed of locomotion is widely believed to increase organismal fitness by enhancing the ability of animals to escape predators, capture prey, and defend territories (Hertz et al. 1988; Garland and Losos 1994). As a consequence, physiological

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ecologists have frequently studied sprinting speed to gain insights into the causes and consequences of variation in organismal performance. Organismal performance is a complex result of physiological capacity, environment, morphology, and behavior. Thus, maximum sprinting performance has been studied from the diverse perspectives of how factors such as muscle physiology, temperature, and limb dimensions may constrain or affect performance (e.g., Bennett 1982; Marsh and Bennett 1986; Miles 1994). Lizards have frequently served as a model organism for such studies of sprinting speed, which is typically determined using level racetracks 1–3 m long and standardized laboratory conditions (Bennett and Huey 1990; Garland and Losos 1994).

The lack of corroborative field observations of sprinting speeds of lizards may complicate determinations of the ecological relevance of laboratory tests for several reasons. For example, physiologists often assume that animals fleeing from predators in nature do so at maximum speed. However, this assumption is largely untested, and an equally plausible alternative is that animals use only the minimal speed needed to escape. In addition, few studies have examined whether the escape distances of lizards in the field are similar to the lengths of racetracks that are used in the laboratory (Martin and Lopez 1995; Jayne and Ellis 1998). Natural habitats also commonly are complex in structure and have surfaces of varying inclines, but only one field study (Jayne and Ellis 1998) has determined the extent to which lizards run in a straight line and on surfaces of varying incline.

Compared with many other structural attributes of terrestrial environments, inclines have predictable mechanical consequences for locomotion. If a lizard travels identical distances on uphill and level surfaces, movement on the incline requires more work to lift the mass of the animal, and the net cost of transport increases (Farley and Emshwiller 1996). Running up inclines also may measurably decrease maximum speed of large but not small lizards, which led Huey and Hertz (1984) to suggest that small (<30 g) lizards could enhance their ability to escape larger lizards by running uphill. Equally plausible alternative hypotheses might negate the prediction that small lizards will run uphill during escapes. For example, lizards may travel a path directly away from a potential predator regardless of the incline encountered. Similarly, lizards might run toward the nearest available refuge regardless of its orientation with respect to either incline or the location of the predator.

The occurrence of inclines in a natural environment and the extent to which locomotion occurs on inclines have only been

determined previously for a single species of lizard. Jayne and Ellis (1998) studied the escape locomotion of the Mojave fringe-toed lizard, *Uma scoparia*, in a sand dune habitat where surfaces were as steep as 32°, which is the angle of repose of this loose sand. Unlike other genera in the well-defined clade of lizards to which it belongs (de Queiroz 1992), *U. scoparia* is restricted to habitats with loose sand, and the fringes formed by scales on its toes are a morphological specialization that enhances running speed on loose sand (Carothers 1986). Irschick and Jayne (1998) recently found that sprinting speeds of *U. scoparia* up a 30° incline were not significantly different from those on a level surface in laboratory tests, whereas the speeds of a closely related species, *Callisaurus draconoides* (Blainville), were adversely affected by incline in the laboratory.

Comparing the locomotor performance of *C. draconoides* with that of *U. scoparia* is of interest for several reasons. First, the two species are closely related (de Queiroz 1992) and have similar overall size, but the legs and tail of *C. draconoides* are relatively longer (Irschick and Jayne 1998) in a fashion that resembles the morphology of many lizards species that are considered bipedal specialists (Snyder 1962). Thus, field observations of both species should provide insights regarding the relationship between bipedality and sprinting performance. We have observed both *C. draconoides* and *U. scoparia* in the same sand dune microhabitat, even though *C. draconoides* occurs most commonly in microhabitats such as rocky and sandy washes (Stebbins 1985; Hasson et al. 1989). Finally, the species-dependent effects of incline found in laboratory tests of *U. scoparia* and *C. draconoides* (Irschick and Jayne 1998) led to the prediction that to avoid a decrement in performance *C. draconoides* should avoid running up inclines during escape locomotion in its natural habitat.

We examined how incline affected the escape locomotion of the lizard *C. draconoides* in the field. We chose the sand dune habitat for several reasons. First, the dune surface has a simple enough structure that we could quantify the frequency distribution of available inclines in the environment. Second, the soft dune surface accurately preserves the footprints of running lizards, thus allowing quantification of many attributes of escape locomotion, including estimates of maximal speed. Third, the dune study site is an area where *C. draconoides* and *U. scoparia* cooccur, and hence, interspecific comparisons of field escape performance have few confounding habitat factors. Last, this system provides a unique opportunity to determine how often bipedal running is used in nature and how bipedality relates to incline or aspects of sprinting performance such as velocity.

We examined escape sprinting performance of *C. draconoides* in the field to answer the following questions: (1) Does *C. draconoides* sprint near maximal speed when evading a threat in nature? (2) Does *C. draconoides* avoid escaping up inclines? Alternatively, does *C. draconoides* escape randomly with respect to incline yet suffer a decrement in sprinting performance on

inclines in nature? (3) How often does *C. draconoides* run bipedally in nature, and how is bipedality related to sprinting performance? (4) How similar are field and laboratory performance? Finally, we discuss how the escape tactics and field sprinting performance of *C. draconoides* compare with those of *U. scoparia*.

Material and Methods

Study Site

All field observations occurred in the Kelso dune system of the Mojave desert approximately 20 km southwest of Kelso in San Bernadino County, California, approximately 6 km west of the site of Jayne and Ellis (1998), which was in the same dune system. The study site was approximately 1 km × 200 m (between 34°52.967′N, 115°44.679′W, and 34°52.942′N, 115°42.293′W), and the study area was nearly parallel to the edge of the dune and approximately 20 m north of a wash. Vegetative cover was primarily from two species of plants, *Croton californicus* and *Petalonyx thurberi*, which were often on top of distinct mounds of sand. In addition, *Callisaurus draconoides* occasionally used creosote bushes (*Larrea tridentata*) as escape retreats on regions of the sand dune that were adjacent to a nearby wash. Most permanent burrows, used by lizards as refugia, were at the base of such clumps of vegetation, since the sand in areas lacking vegetation generally could not support openings large enough to accommodate the locally occurring species of lizards. Subjectively, vegetation appeared similar to that of nearby sites, for which the percentage of vegetative cover varies from 0.85% to 12.68%, depending on the portion of the dune (B. Jayne, M. Sanwald, and D. Irschick, unpublished data). Grasses usually composed about half of the vegetative cover, with large shrubs and bushes forming the other half (B. Jayne, M. Sanwald, and D. Irschick, unpublished data).

We used two methods to determine the occurrence of inclines in the study area. First, to gain an overall perspective on the topography of the dune surface, we measured inclines for every meter along two 200-m transects, one at each end of the study site. Second, along a straight line through the study site (960 m), we used a digital level on a 1-m rod to measure the maximum incline of the ground at locations 10 m apart, where the orientation of the rod for each measurement was in the direction of the steepest incline rather than necessarily being parallel to the edge of the study area. The 96 resulting angles of maximal inclination were transformed into the rise per meter (RISE) by multiplying the sine of the angle by 1 m. For any inclined plane, an infinite number of lines (and slopes) pass through a single location; however, the inclines of all these lines are between plus and minus the maximum slope of the inclined plane. As a consequence, for each of the 96 intervals of plus and minus maximal RISE, we used a spreadsheet function to generate four random samples. The resulting frequency distribution ($n =$

384) reflects the probability of a particular slope for a random 1-m trajectory of an animal traversing the dune within the study area and, thus, can be used to generate the expected frequencies of incline for a random path in this environment.

Field Measurements of Escape Locomotion

Fieldwork was from July 3 to 22, 1997, and on each day we searched for lizards and footprints during approximately 0830–1130 hours and 1630–1930 hours. Over the entire study, we quantified footprints for 30 complete escape paths. To avoid any systematic bias in whether we were uphill or downhill of an escaping lizard, we searched for lizards by walking haphazardly within the study area. We typically sighted lizards once they had begun to flee, and we made no attempt to pursue the lizards until they had stopped running. We were able to capture five *C. draconoides* for which snout-vent length averaged (± 1 SD) 7.1 ± 0.5 cm and ranged from 6.3 to 7.6 cm. Body mass averaged 10.1 ± 2.5 g and ranged from 6.8–13.5 g.

We used surveyor flags to mark 1-m straight-line distances along each escape path. We then used a digital level ($\pm 0.1°$) to measure the angle of the incline rounded to the nearest one-half degree. We transformed each angle into values of RISE, as was done for the habitat sample. We then calculated the total amounts of uphill (UP) and downhill (DOWN) change in vertical position along the entire path, and UP $-$ DOWN yielded the net vertical gain (NET) from the beginning to the end of the entire path. Vertical gains are useful quantities because they are proportional to change in potential energy and the additional mechanical work required to traverse an incline compared with an identical distance on a level surface. Because the steepness of inclines on a path may vary in a complex fashion, however, vertical gains convey almost no information about the distances that are traveled on inclines. Thus, we also calculated the percentage of the 1-m intervals that had positive (%UP) and negative (%DOWN) vertical gains, and because some intervals were horizontal ($0° \pm 0.5°$), %UP + %DOWN did not always equal 100%. We also measured the maximum incline of the substrate (in any direction) at the midpoint of each 1-m interval along the escape path.

We recorded whether the end of each path was (1) an exposed location (neither under vegetative cover nor within a burrow), (2) under vegetative cover, or (3) a permanent burrow. To be considered cover, the minimum diameter of a clump of vegetation had to exceed the approximate total length of the lizards (15 cm) and be dense enough to effectively obscure our view of an animal behind or beneath it. We categorized each stride (distance traveled between successive footprints of the right hindfoot) as either quadrupedal or bipedal by examining whether forelimb footprints were present. Previous laboratory observations of sprinting *C. draconoides* (Irschick and Jayne 1998) revealed that the fore- and hindfeet generally do not land at the same point, except occasionally during the first few strides of rapid accelerations. As a consequence, with only a few exceptions, we could reliably categorize each stride within a path as quadrupedal or bipedal. We used a ruler (± 1 mm) to measure the length of each stride in a path directly from footprints in the sand.

We also used compass bearings ($\pm 2°$) to determine the orientation of (1) each 1-m interval of the escape path, (2) the starting to the end points of the entire path, (3) the point at which an observer noticed the fleeing lizard to the starting point of the path, (4) the starting point of the path to the nearest available cover, and (5) the steepest incline measured over 1 m and centered at the midpoint of each meter of the path.

We subtracted pairs of angles indicating orientation to calculate five variables that quantified the trajectories of the escapes, and each trajectory variable was standardized to allow values to be pooled meaningfully and analyzed with circular statistics (Zar 1996). ALL $-$ M1 is the difference between the trajectory of the entire path versus the trajectory of the first meter of the escape path. ALL $-$ OBS and M1 $-$ OBS indicate the trajectories of the entire path and first meter, respectively, relative to the observer so that $0°$ indicates movement directly away from the observer. M1 $-$ COV indicates the trajectory of the first meter of the path relative to the nearest available vegetative cover so that $0°$ indicates movement directly toward the nearest cover. AVOID indicates the difference between the direction of travel and the steepest available incline so that $0°$ indicates running directly uphill. The first meter of the escape path was of particular interest because this is where most acceleration occurs and was usually where the lizard was closest to the threat.

We also quantified approach distance (APPROACH) as the straight-line distance between the observer and the start of the path. LENGTH was the path length as measured by summing up all meters in an escape path. To clarify how convoluted the escape path was, we also measured the straight-line distance between the start and end points of the entire path (STRAIGHT) and compared these values with LENGTH.

We used a thermocouple and a Fischer digital thermometer to obtain temperatures ($\pm 1°$C) of the air at chest height in the shade (mean $\pm$ SD = $33.9° \pm 3.5°$C, min = $26°$C, max = $39°$C, $n = 30$) and ground surface (mean = $42.7° \pm 5.1°$C, min = $34°$C, max = $52°$C, $n = 30$) at the starting point of all escape paths. When possible, we measured the cloacal temperatures of lizards that we were able to capture soon after sighting (mean = $38.8° \pm 2.2°$C, min = $36°$C, max = $42°$C, $n = 5$).

Results

Habitat

Inclines are abundant on the surface of the sand dune both as a result of relatively small mounds (basal diameter 1–3 m;

height <1.5 m) on the dune surface, associated with clumps of vegetation, and larger scale undulations of the dune surface that commonly extend more than 10 m (Fig. 1). Figure 2*A* shows the frequency distribution of the maximal values of RISE measured at 10-m intervals for a 960-m straight line through the rectangular study area. For the 96 measurements of RISE on the transect, the greatest value of RISE per meter of the dune surface was 0.46 m (27.5° incline), but we observed other surfaces in the habitat that had inclines of 32° (RISE = 0.54), which approximates the angle of repose for loose sand in the dune habitat. The mean and median values of maximal RISE were 0.17 and 0.15 m, respectively. Figure 2*B* shows the frequency distribution of the random sample of 384 slopes, for which neither the mean (0.0042 m) nor the skewness (0.116) was significantly different from zero ($t = 0.74$ and 0.95 respectively, $P > 0.20$ in both cases). However, the kurtosis (1.02) of the random sample (Fig. 2*B*) was significantly greater than zero ($t = 4.16$, $P < 0.001$).

Escape Paths

Figure 2*C* shows the frequency distribution of all values ($n = 326$) of RISE per meter that were measured for the 30 escape paths. The mean ± SD value of RISE of escape paths was 0.009 ± 0.110 m. Neither the mean nor the skewness (0.0042) of this distribution were significantly different from zero, but the kurtosis of the distribution (0.79) was significantly greater than zero ($t = 2.92$, $P < 0.05$), indicating leptokurtosis. Because of the leptokurtosis, parametric tests such as a *t*-test comparing means with the random sample of habitat could be inappropriate. Therefore, we performed a Kolmogorov-Smirnov goodness-of-fit test for continuous grouped data (Zar 1996, p. 478) and detected a significant difference between RISE for the random sample and the escape paths ($d_{max} = 63.24$, df = 26, 326, $P < 0.001$) such that the escape path distribution of RISE had slightly more positive small RISE values than the random distribution (Fig. 2).

Table 1 summarizes several attributes of entire escape paths. The lengths of escape paths ranged from 1.3 to 37.6 m and averaged 10.8 m (Table 1). Escape paths were quite straight, as indicated by values of STRAIGHT averaging (±SD) 95% ± 6.8% of the values of LENGTH. APPROACH distance averaged 3.5 m and was not significantly correlated with path length (Pearson $r = -0.18$, df = 28, $P > 0.25$). Of the 30 escape paths, 18 ended under vegetative cover, four ended in a permanent burrow, and 12 ended at exposed locations. When lizards ran into burrows that were under bushes, we considered these escapes as running *both* to burrows and cover. Path length was not significantly correlated with distance to nearest cover (Pearson $r = 0.27$, df = 28, $P > 0.15$).

The mean (±SD, range) percentages of meters per path that were oriented uphill and downhill were 52% ± 28% (0–100) and 41% ± 28% (0–100), respectively. The mean amounts of uphill and downhill change in vertical position per escape path were 0.51 ± 0.61 m (0.00–2.26) and 0.44 ± 0.59 m (0.00–2.09), respectively. The mean NET change per escape path was 0.07 ± 0.64 m (−1.41 to 1.80). Values of both UP and DOWN increased significantly with path length, whereas values of NET were not correlated with path length (Fig. 3). Within each escape path, the amounts of uphill and downhill locomotion were similar, as indicated by the lack of significant differences between %UP and %DOWN (two-tailed paired *t*-test, $t = .06$, df = 29, $P = 0.29$) and between UP and DOWN ($t = 0.59$, df = 29, $P > 0.50$). Four of the 30 paths consisted entirely of uphill running, and only one path was composed entirely of downhill running.

Figure 4 summarizes values of five trajectory variables for the 30 escape paths. The orientations of the overall path and the first meter were usually similar, as indicated by a nonuniform distribution (Rayleigh's test for circular uniformity, $Z = 20.03$, $P < 0.001$; Fig. 4*A*) and an angular mean value of ALL − M1 that was not significantly different from 0. The values indicating the trajectory of the first meter of the path relative to the observer had only a marginally significant deviation
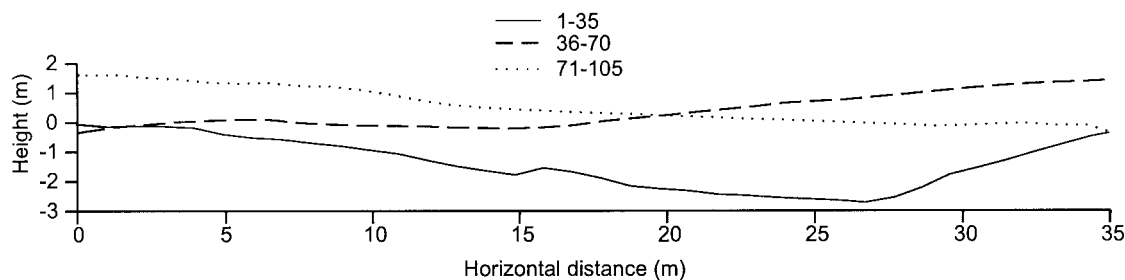

Figure 1. Elevation profile of the dune surface for three contiguous 35-m segments taken from a 200-m transect. The vertical and horizontal scales are the same so that the slopes of the lines accurately convey inclines in the habitat. Height is relative to the starting point of the transect.
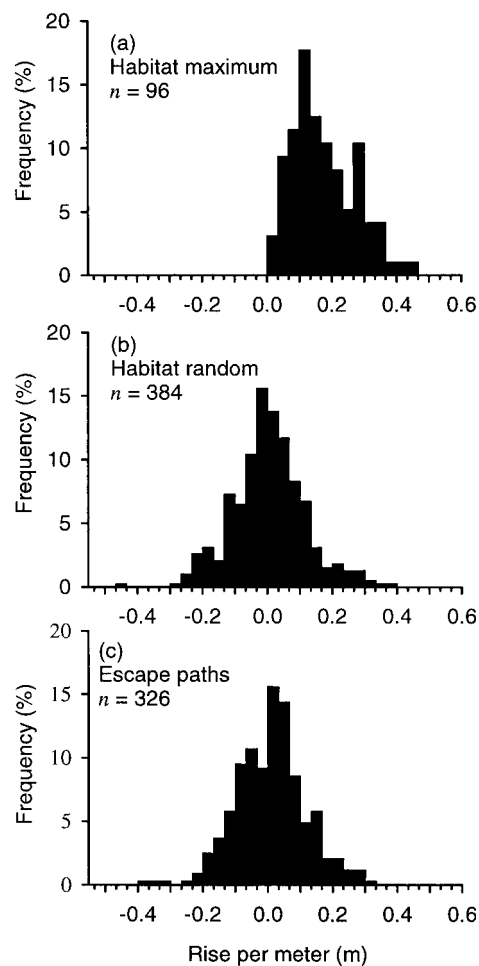
Figure 2. Frequency distributions for values of RISE per meter. *a*, Maximal values measured at 10-m intervals along one 960-m transect. *b*, A random sample of 384 values derived from the distribution shown in *a*. *c*, All values for each meter of 30 escape paths.

from a uniform circular distribution ($Z = 3.28$, $0.02 < P < 0.05$; Fig. 4C). The trajectory of the entire path relative to the observer did not differ significantly from a uniform distribution ($Z = 2.00$, $P > 0.10$; Fig. 4B). The trajectory of the first meter relative to nearest vegetative cover was nonrandom, with a mean value that was directed toward nearest cover ($Z = 7.03$, $P < 0.01$; Fig. 4D). Because lizards tended to run initially toward nearest vegetative cover, a bias in the location of nearest vegetative cover relative to the observer potentially could bias orientation of the first meter of running relative to the observer. However, because values of the angle between the vectors from the lizard to the nearest vegetative cover and from the lizard to the observer had a uniform circular frequency distribution ($Z = 0.31$, $P > 0.50$; not shown in Fig. 4), no bias in the location

of nearest vegetative cover relative to the observer was evident. The trajectory of the first meter of the escape was random with respect to orientation of the steepest incline ($Z = 2.32$, $P > 0.05$; Fig. 4E).

Of 301 turns that were measured between successive 1-m intervals within 30 escape paths (Fig. 5), only 5.0% of the turn amplitudes were greater than 45°, and 37.4% of the turn amplitudes were less than or equal to 5°. We found no consistent trends comparing the amount of turning per 2 m for the beginning versus the final 2 m of the path or for the middle portions of the path versus the beginning and end. The mean ± SD number of times that a lizard switched from a left to right turn within a path was 4.3 ± 3.8 (range = 0–15), and the number of switches within a path had a highly significant positive correlation with path length (least-squares regression slope = 0.392, intercept = 0.059, $r^2 = 0.86$, df = 28, $P < 0.001$).

Stride Length, Bipedality, and Effects of Incline

Maximum stride length per path ranged from 21.0 to 52.0 cm with a mean ($n = 30$) value of 35.8 cm. For all 877 strides, the mean value of absolute stride length was 24.4 cm. For the frequency distribution of all relative stride lengths (percentage of maximum within a path), the modal bins were from 70% to 80% (Fig. 6A). Nearly one-fourth (23.1%) of the cumulative number of strides were less than or equal to 50% of the maximum length, and 34.9% and 11.6% of the strides had values of relative length exceeding 75% and 90%, respectively (Fig. 6A). The frequency distributions of relative stride lengths for bipedal and quadrupedal strides were significantly different (Kolmogorov-Smirnov test, $d_{max} = 99.4$, df = 18,268, $P < 0.001$), primarily as a result of bipedal strides being longer than quadrupedal strides (Fig. 6).

Of the 877 strides measured, 30.6% were bipedal. Overall, only 3.3% of the bipedal strides occurred singly, 8.5% were in consecutive pairs, 23.3% were in consecutive series between five and 10 strides, and 64.9% were in consecutive series greater than 10 strides. Therefore, *Callisaurus draconoides* frequently exhibited long, unbroken stretches of bipedal running rather than intermittent use of bipedal and quadrupedal running.

We also examined how mean stride length and percentage of bipedality changed from the first ($n = 30$) to the twenty-seventh stride ($n = 10$). The mean ± SD relative length of the first stride was 41% ± 4% of the maximum attained within each escape. As lizards accelerated, each successive value of mean relative stride length increased up to the fourteenth stride (mean cumulative path distance = 3.04 m, mean relative stride length = 73%), after which no further conspicuous increases were apparent (Fig. 7A). The percentage of strides that were bipedal also generally increased with stride number until about the fourteenth stride (Fig. 7B). As a consequence, the per-

Table 1: Summary statistics (mean, range, SD) for escape locomotion of lizards in a sand dune habitat

Variables	*Callisaurus draconoides* Mean (Range)	SD	*Uma scoparia* [a] Mean (Range)	SD
LENGTH (m)	10.8 (1.3–37.6)	9.1	10.6 (1.7–34.0)	6.8
APPROACH (m)	3.5 (.3–12.3)	2.6	4.2 (.3–20.5)	4.7
Mean STRIDE (cm)	23.7 (13.9–38.4)	5.5	20.7 (13.8–27.2)	3.5
Maximum STRIDE (cm)	35.8 (21.2–52.0)	7.7	30.0 (18.5–39.8)	6.2
Maximum speed (m/s)[b]	4.10 (2.54–5.82)	1.13	3.62 (2.29–4.61)	.74
Distance to cover (m)	6.5 (.2–26.1)	7.5	1.5 (.3–4.0)	1.1
TURN (degrees)[c]	15.4 (0–80)	15.0	13.3 (0–88)	14.1
Meters bipedal (%)[d]	42.9	...	10.0	...
End in burrow (%)	13.3	...	55.8	...
End in cover (%)	60.0	...	59.6	...

Note. All variables except for TURN and percentage of meters bipedal, which are per meter quantities, are means of escape paths by each lizard ($n = 30$ and $n = 29$ for *Callisaurus draconoides* and *Uma scoparia*, respectively).

[a] Jayne and Ellis (1998).

[b] Calculated using regression relating stride length to speed (Irschick and Jayne 1998).

[c] Values of TURN are absolute values .

[d] Percentage of meters that have at least one bipedal stride.

centage of bipedal strides had a significant positive correlation with mean relative stride length (Pearson $r = 0.74$, df $= 25$, $P < 0.001$). The distance at which maximum stride length was attained within each path had a significant positive correlation with path length (Fig. 8).

We used a combination of simple and multiple regression analyses to attempt to clarify the factors that affected mean relative stride length per meter. The amount of turning between successive meters had no significant predictive value for mean relative stride length in any regression model. The regression model that explained the most variance had a quadratic term of RISE of the path as the independent variable with a significant regression coefficient ($r^2 = 0.034$, df $= 238$, $P < 0.005$). The significant relationship between mean relative stride length and RISE^2 was primarily a result of the first meter of the escape paths as indicated by the lack of any significant correlations when data from the first meter were excluded from the regression analyses. When mean relative stride lengths of only the first meter were analyzed, RISE^2 had a significant negative relationship with mean relative stride length ($r^2 = 0.18$, df $= 27$, $P < 0.025$), and this did not appear to be a result of the values of RISE for the first meter being unusually large relative to values for remaining meters. Thus, overall, incline had little explanatory power for a decrement in locomotor performance as indicated by the analyses of relative stride length.

The orientation of escape running relative to the direction of the steepest incline (AVOID) depended on the steepness of the surface on which the lizard was running (Fig. 9). On shallow slopes (Fig. 9A), lizards often ran directly downhill (180°) or uphill (360°) in addition to running horizontally (90° and 270°).

In contrast, on steep slopes, lizards avoided running directly downhill and uphill and escaped almost exclusively by running horizontally (Fig. 9B). A Kolmogorov-Smirnov test comparing observed values for steep slopes versus those based on the shallow slopes showed that the two distributions were significantly different ($d_{max} = 10.97$; df $= 18, 59$; $P < 0.05$).

Discussion

Field and Laboratory Performance

An important issue in physiological ecology is how organisms perform in the laboratory versus in the field (Hertz et al. 1988; Pough 1989; Garland and Losos 1994). Studying field performance is important because if organisms do not perform maximally in nature, then selection cannot operate on maximal capacity for performance (Irschick and Losos 1998).

Two methods allow us to integrate our field measurements of maximal stride length with laboratory observations to estimate the maximal speeds obtained by *Callisaurus draconoides* in the field. For running on sand in the laboratory, Irschick and Jayne (1998) found stride durations of both *C. draconoides* and *Uma scoparia* do not change dramatically after the fifth stride during accelerations from a standstill. Dividing maximal stride length of each path ($n = 30$) in the field by the mean duration (0.081 s) of the fifth stride observed in the laboratory (Irschick and Jayne 1998) yields estimates of maximal velocities in the field ranging from 2.59–6.41 m/s with a mean ± SD value of 4.42 ± 0.95 m/s. Using regressions relating speed and stride length in the laboratory (Irschick and Jayne 1998) with
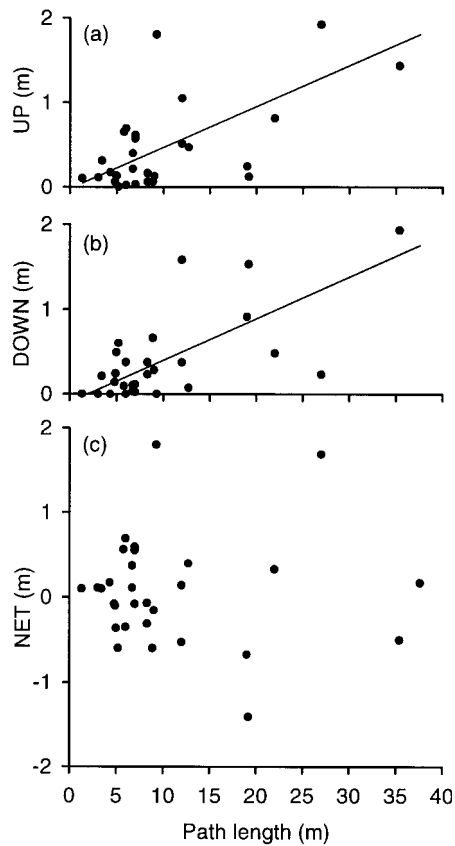
Figure 3. Amounts of change in vertical position versus length of each escape path ($n = 30$). Regressions are shown only for significant relationships. *a*, Total uphill, UP $= -0.017 + 0.048 *$ LENGTH ($r^2 = 0.53$, $P < 0.001$). *b*, Total downhill, DOWN $= -0.09 + 0.049 *$ LENGTH ($r^2 = 0.58$, $P < 0.001$). *c*, NET change ($r^2 = 0.001$, $P > 0.25$).

values of maximal stride length per path in the field for *C. draconoides* yields very similar estimates of maximal velocities in the field ranging from 2.54–5.82 m/s with a mean $\pm$ SD value of 4.10 $\pm$ 1.13 m/s.

Average maximal velocity (3.54 m/s) observed for the level laboratory trials of *C. draconoides* (Irschick and Jayne 1998) was either 80% or 86% of estimated field values, depending on the method used to estimate field values. Similarly, for *U. scoparia* (Jayne and Ellis 1998) the average laboratory value was from 71% to 77% of the average estimated maximal speeds in the field (3.96 and 3.62 m/s). The different tendencies of the two species to run directly to nearest cover may partially explain the tendency of *C. draconoides* to run nearer its maximum than *U. scoparia* in the laboratory. Irschick and Jayne (1998) used an artificial shelter at one end of the racetrack in the laboratory, and nearly all of the *C. draconoides* ran directly into this shelter,

whereas *U. scoparia* did this in only about one-half of the trials. In the field, the location of nearest vegetative cover had significant predictive value for the trajectory of *C. draconoides*. However, nearest vegetative cover had no predictive value for the direction of *U. scoparia* in the field, and some additional details led Jayne and Ellis (1998) to suggest that this species usually escapes toward a familiar retreat. Thus, the visual stimulus at the end of a racetrack in the laboratory was sufficient for eliciting very rapid locomotion in *C. draconoides*, whereas *U. scoparia* may be behaviorally inhibited from running rapidly in the laboratory because of the lack of a familiar retreat.

Another factor contributing to the slower than maximal speeds of both *C. draconoides* and *U. scoparia* in the laboratory appears to be that the racetrack used in the laboratory trials (3 m long with working area <2 m) was considerably shorter than the average distance at which both *C. draconoides* and *U. scoparia* attained maximal stride length (and speed) in the field (Irschick and Jayne 1998; Jayne and Ellis 1998; present study, Fig. 7). In contrast to maximal stride length for entire escape paths, the mean (± 1 SD) values of cumulative distances traveled during the first five strides of sprinting in the laboratory were actually slightly higher than values obtained in the field for both *C. draconoides* (laboratory: 0.93 $\pm$ 0.13 m; field: 0.83 $\pm$ 0.15 m) and *U. scoparia* (laboratory: 0.69 $\pm$ 0.05 m; field: 0.66 $\pm$ 0.06 m). Thus, field and laboratory estimates of speed are most similar when compared over equivalent distances.

Irschick and Losos (1998) recently found that *Anolis* lizards in nature use approximately 90% and 70% of their maximal locomotor capabilities during escape and feeding, respectively. Average lengths of escape paths (ca. 50 cm) of *Anolis* lizards in the field were similar to the lengths of sprints obtained in the laboratory, and the field escape speeds never exceeded laboratory values (Irschick and Losos 1998). Because *C. draconoides* and *U. scoparia* typically run much longer distances in the field than in the laboratory tests, this confounds direct comparisons of our findings for sprinting performance in the laboratory versus field with those of Irschick and Losos (1998). However, the limited available data for lizards suggest that when the confounding effects of distance are controlled for, laboratory sprinting performance can slightly exceed field sprinting performance, and two conditions that might enhance laboratory performance are more predictable footing and closer proximity of the threat (investigator) on laboratory racetracks.

Conveniently, the average lengths of field escape paths of *C. draconoides* and *U. scoparia* are almost identical (Table 1), and hence escape distance does not pose a confounding factor for comparing sprinting speeds of these species. Compared with *U. scoparia*, the mean values of maximal field (Table 1) and level laboratory (Irschick and Jayne 1998) speeds of *C. draconoides* were approximately 11% and 21% faster, respectively. Thus, despite some similarities in the escape behavior of these two closely related species (Table 1), one should not overlook
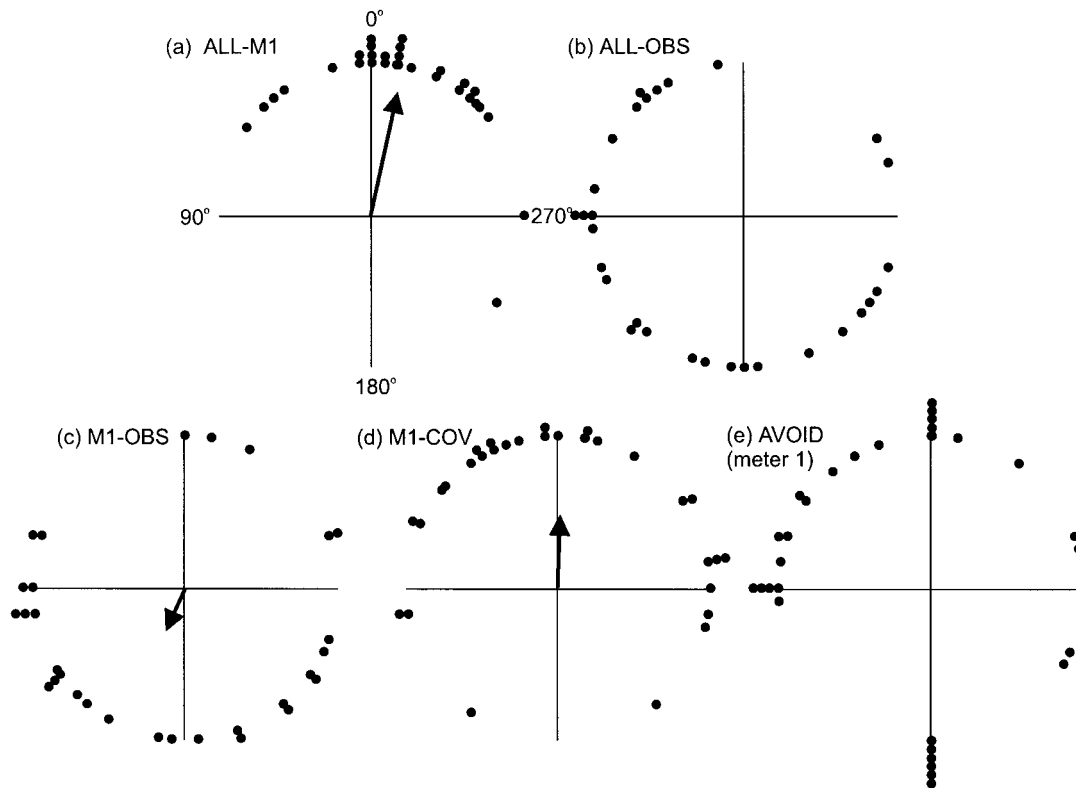
Figure 4. Angular frequency distributions for the trajectories of the 30 lizard escapes observed. For distributions that were not uniform, the direction of the arrows indicates the angular means, and the length of the arrows is inversely proportional to the dispersion of the data. *a*, The difference in trajectories between the end points of the entire path (ALL) and the first meter of the path (M1), such that 0° indicates identical trajectories. *b, c*, Trajectories of the entire path and first meter of the path, respectively, relative to the location of the observer (OBS), such that 0° indicates running directly away from the observer. *d*, Trajectories of the first meter of the path relative to the location of the nearest vegetative cover (COV), such that 0° indicates running directly toward the nearest cover. *e*, Trajectories of the first meter of the path relative to the steepest uphill path (UP), such that 0° indicates running directly uphill.

the differences in the absolute speeds that they attain. *Uma scoparia* only occurs on loose sand and has many morphological specializations for living on loose sand (Stebbins 1944), including toe fringes that enhance running speed on loose sand (Carothers 1986). As a consequence, one might expect that *U. scoparia* would run faster on loose sandy substrates than the population of *C. draconoides* that we examined, which lack toe fringes. Interestingly, a Baja population of *C. draconoides* has toe fringes (Luke 1985). Contrary to expectations, however, *C. draconoides* sprints more quickly than *U. scoparia* on loose sandy substrates in both the laboratory and the field.

An additional important finding for *C. draconoides* in nature was that only a small fraction (11.6%) of escape locomotion was near (i.e., 90%) maximal running speed (Fig. 6), even though *C. draconoides* achieved greater absolute speeds in the field than in the laboratory. This finding may support Hertz et al. (1988), who suggested that reptiles may be more like boy scouts than Olympic athletes: they are always prepared but do not always give an all-out effort.

Effects of Incline on Escape Performance

Explaining why we detected a negative effect of incline on the stride length (and velocity) of *C. draconoides* only over the first meter of their escape paths poses a challenge. In contrast to the case for *C. draconoides*, inclines in nature (excluding the first meter of escape paths) had a significant negative quadratic effect on *U. scoparia* such that stride lengths were greatest for paths that were horizontal (i.e., RISE = 0; Jayne and Ellis 1998). The nature of incline effects on *C. draconoides* might reflect complicated interactive effects of incline and acceleration on the velocity of this long-legged species since the greatest accelerations are generally confined to the first meter of an escape path. Alternatively, a lack of running up or down steep inclines
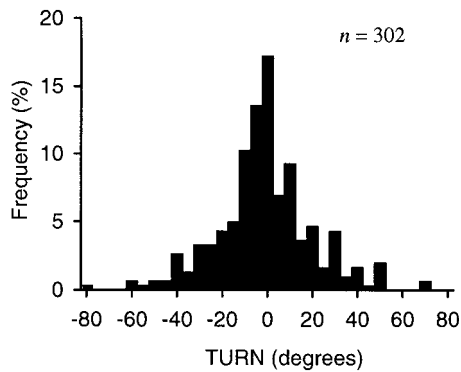
Figure 5. Frequency distribution for the amount of turning between each successive 1-m interval for all meters of each path. Positive values represent right turns, and negative values represent left turns. Mean ± SD = −1.06° ± 21.3°. Skewness = 0.064. The mean of this distribution is not significantly different from 0 (t-test, $t = 0.86$, $P >$ 0.05).

simply might restrict the range of values of path incline sufficiently so that regression analysis would be unlikely to detect a significant effect of incline on stride length similar to that found for *U. scoparia*. Since steep (>15°) surfaces are relatively rare, little statistical power is available for detecting differences between the observed and expected frequencies of steep path inclines (Fig. 2*B*, *C*). The orientation of escape paths relative to the available inclines indicated that *C. draconoides* avoided running directly uphill when on steep slopes, and this behavior could contribute to the rarity of steep path inclines needed to detect significant effects of incline on performance. Furthermore, this sort of incline avoidance by *C. draconoides* may be a threshold response rather than a simple continuous function (Fig. 9).

Assuming that the conditions that increase the energetic cost of locomotion also decrease maximal possible speed, then some insights into the effects of incline might be gained from studies of the energetics of locomotion. For example, previous studies of vertebrates, including small lizards, have demonstrated that the net cost of transport increases when animals move up steep inclines (Taylor et al. 1972; Farley and Emshwiller 1996). Thus, the avoidance of running directly up steep inclines by *C. draconoides* does not seem surprising. In contrast, we did not expect to find an avoidance of direct downhill running by *C. draconoides*. Interestingly, the energetic cost of human locomotion is minimized on 10% downhill grades, and energetic cost increases for increasingly steep downhill locomotion (reviewed in McMahon 1984). Thus, some aspects of running down a steep incline may impede the physiological capacity to run rapidly.

Several cautionary notes are in order regarding these inferences for the locomotion of small lizards that are drawn from studies of humans. First, the mass of animals often has pro-

found consequences for how inclines affect locomotion (Taylor et al. 1972; Huey and Hertz 1982, 1984). Second, the physiological attributes of animals that limit maximal speeds are not well understood for locomotion on either level or inclined surfaces. Third, we have no empirical data on the energetic cost of locomotion on loose sand, and loose sand and incline seem likely to have complicated interactive effects on the energetic cost of locomotion. Finally, the reluctance of some lizards to run down steep hills may be a behavior that is not related to a physiological capacity to run. For example, Jayne and Ellis (1998) could not reliably obtain sprinting of *U. scoparia* down a 30° incline in the laboratory. The paucity of studies of lizard locomotion on inclined surfaces is particularly unfortunate be-
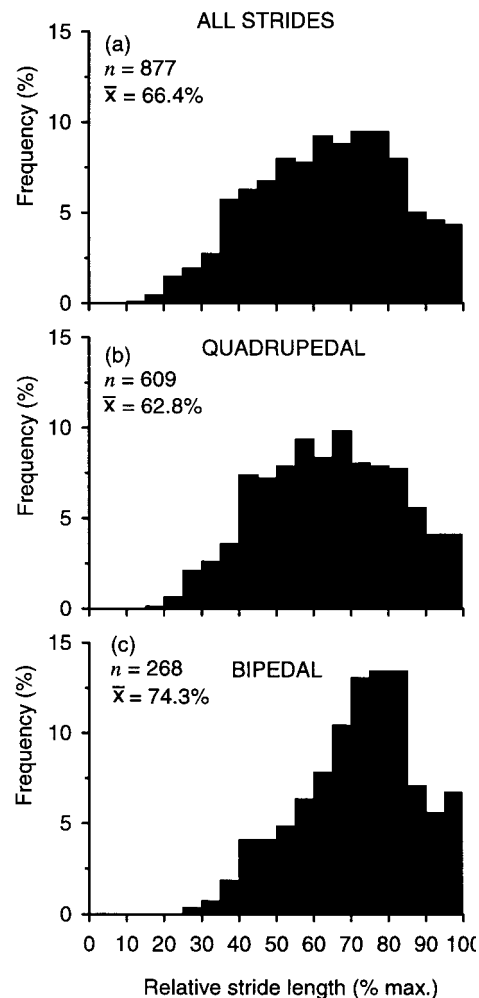

Figure 6. Frequency distribution for relative (% maximum) stride lengths for (*a*) all strides, (*b*) quadrupedal strides only, and (*c*) bipedal strides only. Compared with quadrupedal strides, bipedal strides had a more distinct mode that was at a higher percentage of maximum stride length.
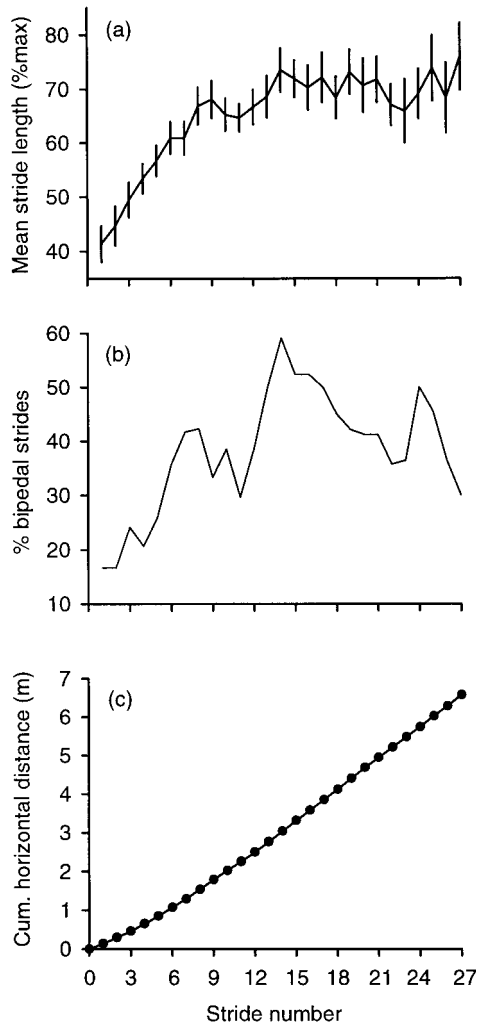
well understood either for lizards or for many other groups of vertebrates (Snyder 1949, 1952, 1962; Djawdan and Garland 1988; Gatesy and Biewener 1991). Lizards are particularly well suited for studying the advantages of bipedal locomotion because its use is not obligate, as is the case for some other groups of vertebrates, such as birds. Previous authors (Snyder 1962) commonly have asserted that bipedal running is faster than quadrupedal running in lizards and that certain lizard taxa such as *Basiliscus* and *Crotaphytus* are bipedal specialists. However, quantitative data on the performance advantages and the propensity for running bipedally are scarce.

Only two studies aside from the present study have quantitatively determined the occurrence of bipedality of lizards. In a laboratory study of the first five strides during sprinting from a standstill, Irschick and Jayne (1998) found that 49% and 20% of the strides were bipedal for *C. draconoides* and *U. scoparia*, respectively. For escape locomotion in the field, 10% of the cumulative number of meters traveled by *U. scoparia* contained bipedal strides (Jayne and Ellis 1998), whereas the present study of *C. draconoides* found a nearly fourfold greater use of bipedality (Table 1). Jayne and Ellis (1998) did not record whether individual strides of *U. scoparia* were bipedal or quadrupedal, but the data for *C. draconoides* (43% vs. 31%) illustrate how the percentage of the meters containing at least one bipedal stride actually overestimates the percentage of strides that were bipedal in *U. scoparia*. Hence, by any of these criteria above, *C. draconoides* is more of a bipedal specialist than its close relative *U. scoparia*.

Considering the advantages of bipedality for locomotor performance is instructive in light of its variable use both within

Figure 7. *a*, Mean (±1 SE) relative stride length (% maximum). *b*, Percentage of bipedal strides versus stride number for data pooled across all escape paths. Sample size for the first stride was 30 and declined to 10 for stride 27 as a result of different lengths of escape paths. *c*, Mean cumulative distance traveled during escape paths versus stride number. Note the correlated increases in relative stride length and the proportion of strides that were bipedal as lizards initially accelerated from a standstill.

cause moving in many directions within a three-dimensional environment is a key attribute for this group of vertebrates. An added incentive for future studies of lizard locomotion down inclines should also come from the fact that what goes up must come down.

Bipedality

Lizards are the only extant reptile group that employs bipedal locomotion, but the advantages of bipedal locomotion are not
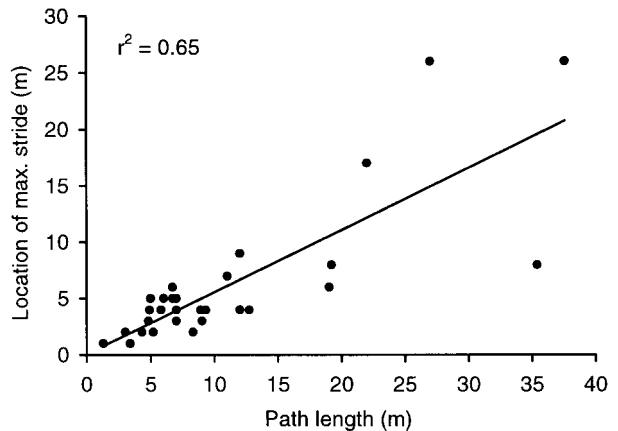

Figure 8. Location of the longest stride within a path versus path length. The slope and intercept of the regression ($r^2 = 0.65$, $n = 30$, $P < 0.001$) are 0.55 and 0.05, respectively. Note that maximum stride length, and hence speed, generally were not attained until sometime after the first 3 m of running, and 3 m exceeds the lengths of most racetracks used to test speed in the laboratory.
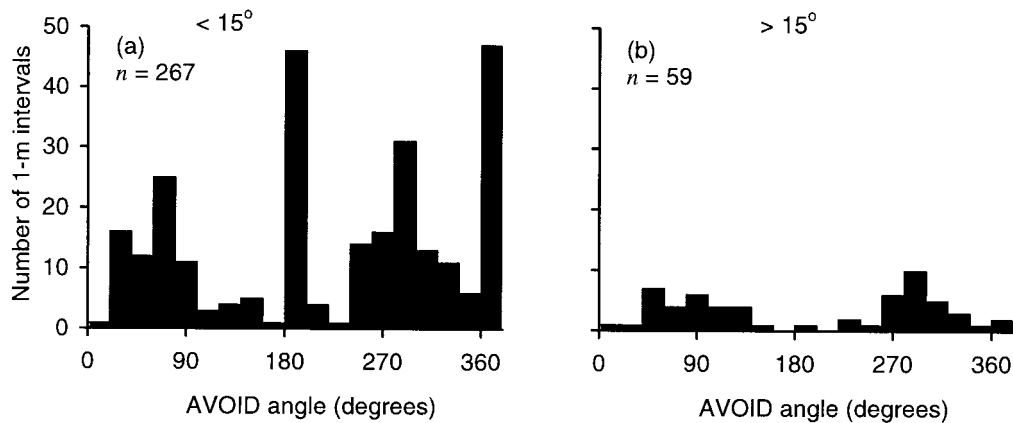
Figure 9. Frequency distributions of AVOID for 1-m intervals that are (*a*) on inclines less than 15° and (*b*) on inclines greater than 15°; 90° and 270° represent running horizontally, and 0° and 180° represent running directly uphill and downhill, respectively. Note the scarcity of running directly uphill or downhill on steep inclines.

and among different species of lizards. Irschick and Jayne (1998) found no tendency for the bipedal strides of *C. draconoides* to be faster than quadrupedal strides. However, considerable acceleration occurs during the first five strides of sprinting from a standstill, and more than five strides are generally required before either *C. draconoides* or *U. scoparia* attains maximal speed. Because acceleration and maximal running speeds are two different metrics of locomotor performance, further insights can be gained from the field escapes by partitioning data into subsets that reflect relatively steady high-speed running or the large accelerations that are largely confined to the first meter of sprinting for both species (Irschick and Jayne 1998). After excluding the first meter of each field escape path, only 4% of the cumulative number of remaining 1-m intervals contained bipedal strides for *U. scoparia* (Jayne and Ellis 1998), whereas this quantity was 44% for *C. draconoides*. Thus, both species often use bipedal locomotion during the initial, accelerating portions of sprinting, but the use of bipedal running by *U. scoparia* for steady high-end speeds is trivial compared with that of *C. draconoides*. The use of bipedal locomotion for steady high-speed locomotion also might be the most useful criterion for characterizing certain species of lizards as bipedal "specialists."

A strong conclusion of the present study was that bipedal strides were commonly longer than quadrupedal strides of *C. draconoides* (Fig. 6), strongly suggesting that bipedal strides are faster than quadrupedal strides. On average, neither stride length nor the probability of bipedality was at a maximum until well after the fifth stride (Fig. 7), which seems the most likely explanation for why Irschick and Jayne (1998) did not detect a speed advantage of bipedal strides in laboratory tests of *C. draconoides*.

If bipedal locomotion is faster than quadrupedal locomotion, then why does *C. draconoides* use quadrupedal locomotion so frequently when escaping? Perhaps quadrupedal strides are primarily a consequence of instability and stumbling during high-speed bipedal running. Our high-speed videotapes of lizards running in the laboratory often show that *C. draconoides* uses its forelimbs after stumbling during bipedal locomotion. The problem of stumbling during high-speed locomotion may not be trivial in a heterogeneous natural environment, such as the Kelso dune site where *C. draconoides* frequently had to run over sparse grass stems as well as irregularities in the surface of the sand during escapes. Furthermore, even on an obstacle-free surface such as a treadmill in the laboratory, we have observed lizards stumbling as a result of a hindfoot bumping into either the tail or the ipislateral forefoot. Thus, lizards may be forced to use a submaximal (quadrupedal) mode of running simply in order to avoid falling.

If *C. draconoides* primarily uses quadrupedal locomotion to regain balance after stumbling during a bipedal stride, then one might expect bipedal and quadrupedal strides to be interspersed rather than having long stretches of continuous bipedal running. However, eight escape paths of *C. draconoides* had more than 10 consecutive bipedal strides, indicating an ability to run bipedally for extended periods without falling. Thus, the extent to which *C. draconoides* deliberately or inadvertently uses quadrupedal locomotion during escapes remains unclear and deserves further study.

Snyder (1962) suggested that the advantages of bipedal running may be most evident in species that have evolved morphological specializations for bipedality, such as long hindlimbs and a long tail. We compared *C. draconoides* and *U. scoparia* because they are closely related, and yet *C. draconoides* has

substantially longer hindlimbs and tail (Irschick and Jayne 1998). Although we found that *C. draconoides* runs faster than *U. scoparia*, disentangling the effects of limb dimensions versus those of bipedality on speed is complicated. Lizards have sufficient behavioral and morphological diversity so that future studies should be able to further test this hypothesis that species with longer hindlimbs attain a greater performance advantage when running bipedally than species with shorter limbs.

Proximate Effects on Field Escape Behavior

Another consideration in studies of locomotion in nature is to understand which environmental factors influence how far and in which direction organisms run. For field escapes of *C. draconoides* and *U. scoparia*, the approach distances, path lengths and amounts of turning were extremely similar (Table 1), but other aspects of how these species interacted with their environment differed conspicuously. For example, the direction of the nearest vegetative cover had the greatest predictive value for the initial escape trajectory of *C. draconoides*, whereas the location of the threat (observer) had little predictive value. In contrast, *U. scoparia* escaped randomly with respect to nearest vegetative cover but predictably ran a path away from the observer (Jayne and Ellis 1998). The distance to nearest vegetative cover from the beginning of an escape path was significantly greater (two-tailed $t = 3.62$, df $= 30$, $P < 0.005$) for *C. draconoides* compared with *U. scoparia* (Table 1). Although both species had similar percentages of escape paths that ended beneath vegetative cover, *U. scoparia* ended escapes much more frequently by running down the openings of burrows (Table 1).

Previous studies of lizards have shown that decreased amounts of vegetative cover increase both escape and approach distances (Snell et al. 1988; Bulova 1994; Martin and Lopez 1995). For Jayne and Ellis's (1998) 100 m × 1 km study site for *U. scoparia*, the percentage of vegetative cover ranges from less than 1% to 13% (B. Jayne, M. Sanwald, and D. Irschick, unpublished data), and the vegetation of our nearby (6 km) study site for *C. draconoides* subjectively appeared similar. The similar escape distances of *C. draconoides* and *U. scoparia* also suggest similar amounts of vegetative cover in the two study sites, but the greater distance of *C. draconoides* to nearest vegetative cover (Table 1) could also reflect the propensity of this species to venture further from dense vegetation.

The robust axial musculature and shorter limbs of *U. scoparia* appear to facilitate active burrowing (sand swimming) of this species (Irschick and Jayne 1998). We and others (Stebbins 1944; Norris 1951) have frequently observed sand swimming by *U. scoparia* in the field, and we have also exploited this behavior to capture several individuals for laboratory studies. Although we have also observed sand swimming of *C. draconoides* in the laboratory, we have never observed this behavior in these slender, long-legged animals in the field (although *C. draconoides* will bury itself into sand during the night, R. An-

derson, personal communication). Further, compared with *C. draconoides*, *U. scoparia* in the Kelso dune system are more closely associated with permanent burrows (not created by sand swimming), as indicated by their use of burrows as escape retreats (Table 1) and as basking sites early in the day. On the one hand, Jayne and Ellis (1998) found that *U. scoparia* typically ran directly toward specific burrows that they used on a regular basis but ignored many other nearby burrows and other available cover (bushes) during their escape runs, suggesting that *U. scoparia* utilizes predetermined escape routes (Stamps 1995). On the other hand, vegetative cover, rather than burrows, may be most important for determining both the initial and overall escape trajectories of *C. draconoides* escape paths.

Acknowledgments

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